

## Integrating the 'genomic mosaic' view of species into studies of biotic interactions: a comment on Bernhardsson *et al.* (2013)

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### Abstract

The co-occurrence of geographical structure in herbivore communities, metabolomes and defence genes in forest trees has been analysed in the context of 'geographical mosaics' of coevolution. A deeper understanding of these important issues will require full integration of a 'genomic mosaic' view of species into community ecology.

### Keywords

Adaptive population divergence, admixture, community genetics, gene flow, genomic mosaic, geographical mosaic theory of coevolution, plant–herbivore interaction, porous genome, recombination, selection.

### TECHNICAL COMMENT

Community genetics has been put forward as the most likely field to integrate the life sciences (Wade 2007), and research on biotic interactions between 'foundation species' such as trees and their associated communities has contributed greatly towards this goal (Whitham *et al.* 2006). In a recent paper in this journal, Bernhardsson *et al.* (2013) convincingly show that the spatial genetic structure of plant defence genes present in a widespread forest tree (*Populus tremula*, the European aspen) co-occurs with the spatial structure in its metabolomes and herbivore communities. This study is important, because it addresses the impact of *within*-species genetic variation on communities and pinpoints possible drivers of the co-evolutionary process, which are topics of great current interest and known relevance to diverse ecosystems throughout the world (Hersch-Green *et al.* 2011; Agrawal *et al.* 2012; Whitham *et al.* 2012). The study also reveals current limits in our ability to analyse and interpret data at the interface of genetics, phenomics and community ecology. We sketch these limitations and suggest how they might be overcome by integrating recent findings from evolutionary genomics into ecology.

Bernhardsson *et al.* (2013) strive to analyse their genetic, metabolomic and community data within the broader framework of the 'geographical mosaic theory of coevolution' (Thompson 2005) and related concepts. This proves difficult, as they find persistent maladaptation of *all* guilds of herbivores to their local hosts, which cannot easily be explained by arms races or temporal mismatching of co-evolving traits (Thompson 2005). 'Information coevolution' of elicitor–receptor interactions (Kniskern & Rausher 2001) also seems an unlikely universal explanation for local maladaptation of herbivores: this would require rapid evolution of effective receptors by the host to "sense" local herbivore guilds, which is debatable considering the long generation time of trees (Kniskern & Rausher

2001), the very recent re-colonisation of the study region (Scandinavia) by animal and plant life, and the stunning diversity of chemical defence mechanisms in *Populus* spp. (Caseys *et al.* 2012; Bernhardsson *et al.* 2013). The difficulties to match results to available theory point to the presence of yet overlooked or under-appreciated drivers of variation in the data.

The key to understanding the patterns encountered by Bernhardsson *et al.* (2013) may lie in recent findings from evolutionary genomics (Arnold 2006; Nosil 2012). We now know that the 'geographical mosaics' experienced by co-evolving sets of species are often complicated by the presence of 'genomic mosaics', which form easily in diverging populations because of great variation in gene flow, spatially varying selection, and drift along the genomes of wild species (Nosil 2012). Such recombinant 'genomic mosaics' will inevitably result in 'phenotypic mosaics' (Arnold 2006), especially in widespread species, including novel combinations of traits with extended phenotypes in communities and ecosystems (Whitham *et al.* 2006; Caseys *et al.* 2012). We must expect that communities structured by such heritable phenotypes respond to intrinsic features of foundation species, in addition to previously modelled aspects of the coevolutionary process. This includes locality-specific variants that arise whenever individual chromosome segments, generated by recombination, spread across populations and experience spatially varying selection (Arnold 2006; Buerkle & Lexer 2008; Nosil 2012). Such locality-specific variants due to 'genomic mosaics' in the host could well explain the consistent trends across herbivore guilds seen by Bernhardsson *et al.*, depending on the genetic architecture of defence traits. A recent study shows that *P. tremula* in Northwestern Europe represents a 'genomic mosaic' between divergent lineages with admixture in Sweden and great variation in the geographical extent of gene flow along chromosomes (de Carvalho *et al.* 2010), which lends support to our argument.

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From a purely technical point of view, fully integrating the ‘genomic mosaic’ view of species into their analysis may allow the authors to “unlock” the strong genetic structure that currently prevents them from clearly pinpointing causative associations (= true positives) between DNA polymorphisms and ecologically important traits. This could be achieved by including the genomic admixture gradient present between their Southern and Northern cluster (de Carvalho *et al.* 2010) into models predicting variation in phenotypic traits and evaluating the genetic ancestry and phenotypic effect of each DNA polymorphism against that gradient. This suite of methods, coined ‘admixture mapping’ in human medical genetics, is currently being adapted to ecology and evolution (Buerkle & Lexer 2008) and has been used to unlock the genetic architecture of ecologically important traits (Malek *et al.* 2012; Lindtke *et al.* 2013). We suspect that this approach holds great potential to shed light on the actual causative links in this co-evolving system, provided that suitable panels of genetic markers and reference populations are identified. The sizes of ‘ancestry blocks’ present in the host’s ‘genomic mosaic’ should facilitate dating of key events in the coevolutionary process. We look forward to seeing future studies that explicitly address the role of ‘genomic mosaics’ in the coevolutionary dynamics of ecological communities.

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